PLANT SPECIES RICHNESS AND ENDEMISM DURING NATURAL LANDSLIDE SUCCESSION IN A PERHUMID MONTANE FOREST IN THE BOLIVIAN ANDES

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Resumen. Se describe la sucesión vegetal y se analiza la riqueza de especies y endemismos de Pteridophyta, Bromeliaceae y Melastomataceae durante la sucesión forestal en deslizamientos naturales en un bosque perhúmedo montano entre 1900-2800 m en el Parque Nacional Carrasco, dpto. Cochabamba, Bolivia. Se reconocieron seis etapas seriales, la primera con especies de briófitas, líquenes y hierbas colonizadoras (etapa 1), las subsiquientes dominadas por hierbas (2), arbustos (3) y árboles pioneros (4) hasta bosque maduro (5) y finalmente bosques senescentes con pocos árboles con dominancia de bambúes y helechos en el sotobosque, que impiden la regeneración de plantas leñosas (6). Bambúes y helechos de la familia Dennstaedtiaceae fueron raros durante la sucesión temprana y aparentemente dependen de suelos orgánicos bien desarrollados y de claros con abundante luz para poder dominar la vegetación en la etapa 6. Todos los grupos de plantas mostraron un aumento en la riqueza de especies desde etapas seriales tempranas hasta las etapas 3-5 y una disminución subsecuente en bosques senescentes. La distribución de la diversidad resultante se corresponde con patrones de mayor riqueza a niveles intermedios de perturbación (si se considera una escala regional) o con edades intermedias (si se considera un punto fijo a través de la sucesión vegetal). Helechos rerresrres, bromeliáceas terresrres y melaramatáceas ruvieron 67%, 50% y 10%, de sus especies resrringidas a etapas 1-3, repectivamente. Este parrón prácticamente no se encontró en especies epífitas. En total, se estima que un 20% de la flora vascular depende de las etapas seriales tempranas. En todos los grupos estudiados, el endemismo fué mayor en las erapas 1-2 y 5, probablemente como resultado de condiciones ecológicas poco estables durante la sucesión intermedia y por causa de desplazamienros competitivos de las especies endémicas en bosques senescentes.

Abstract. Vegetation succession is described and species richness and endemism of Pteridophyra, Bromeliaceae, and Melastomataceae analyzed during forest succession in a perhumid montane forest at 1900-2800 m in Carrasco National Park, dpto. Cochabamba, Bolivia. Six successional stages were recognized, proceeding from barren ground with few colonizing bryophytes, lichens and herbs (stage 1) through srages dominated by herbs (2), shrubs (3) and pioneer trees (4) to mature forest (5), and finally to senescent forest with few canopy trees and a dense understory of bamboos and ferns which suppressed tree regeneration (6). Bamboos and ferns of the family Dennstaedtiaceae were rare during early succession and seemed to depend on well-developed organic soil for their establishment and on abundant light in treefall gaps to attain dominance in stage 6. All plant groups showed an increase in species richness from early successional stages to stages 3-5 and a subsequent decline in senescent forest. The hump-shaped diversity curves correspond to patterns of highest richness at intermediate levels of disturbance (for landslide dynamics on a landscape scale) or intermediate age (for successional dynamics at one spot). Terrestrial ferns, terrestrial bromeliads, and melastomes had 67%, 50%, and 10% respectively of their species restricted to stages 1-3, while almost no epiphytic species showed this pattern. Overall, an estimated 20% of the total vascular plant flora depended on early successional vegetation types induced by landslides. In all study groups, endemism was most pronounced in successional stages 1-2 and 5, perhaps as a result of less stable conditions at mid-succession and due to competitive displacement of endemic species in senescent forest. *Accepted 28 July 1999.*

Key words: Andes, bamboos, Bromeliaceae, endemism, landslides, Melastomataceae, tropical montane forest, Pteridophyta, species richness, succession.

INTRODUCTION

Andean montane forests contain some of the most diverse vegetation communities on earth (Barthlott *et al.* 1996). For example, Ibisch (1996) estimated a total number of about 1000 vascular plant species per hectare in a perhumid montane forest at 2200 m in

Carrasco National Park, Bolivia, which is equivalent to the highest species counts reported for Amazonian lowland forests (Duivenvoorden 1994, Balslev *et al.* 1998). In montane forests a considerable proportion of the species is represented by herbs, shrubs, and epiphytes (Gentry & Dodson 1987), whereas trees and lianas are less diverse than in the lowlands (Gentry 1995).

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Several authors (e.g., Herzog 1923, Stern 1995) have suggested that landslides are important in tropical mountains for maintaining species diversity, particularly in areas with steep topography and a humid climate (Brabb & Harrod 1989). Stern (1995) remarked that landslides "likely contributed to the large portion of forest dominated by colonizing species that are not able to establish or survive under mature, closed-canopy forests" and compared the effect of landslides in the Andes to that of meandering Amazonian rivers, which likewise create a mosaic of successional vegetation types (Foster 1990, Kalliola et al. 1991). Landslides may thus function as a natural disturbance factor, reducing the effect of biotic interactions and creating highly diverse non-equilibrium conditions (e.g., Huston 1979, 1994; Hubbell & Foster 1986).

In spite of the potential role of natural disturbances in maintaining tropical montane species diversity, ecological analyses of landslide disturbances are limited to a few studies in New Guinea (Simonett 1967), Panama (Garwood et al. 1979, Garwood 1985), Puerto Rico (Guariguata 1990), and Ecuador (Stern 1995), in part probably due to difficult access in steep mountainous regions. Most of these studies focus on the early stages of succession, emphasizing the dynamics of colonization and resprouting of uprooted trees and shrubs. In particular, several authors (e.g., Veblen 1989, Stern 1995, Meier 1998) stress the role of bamboos (*Chusquea* and allies) in quickly invading gaps and preventing the regeneration of trees.

Mountains are also well known for their high levels of botanical endemism (Balslev 1988, Barthlott et al. 1996) which is most pronounced on isolated mountain ranges or in areas with special edaphic conditions. It is not known, however, whether at a given location endemic species tend to be concentrated in specific habitats, such as different successional habitats. Among birds, anthropogenically disturbed or degraded forest habitats tend to be occupied by widespread species (the "trash avifauna", see Stotz et al. 1996) whereas endemic species frequently depend on near-natural forests (Laurance & Bierregaard 1997). Similar tendencies have been observed among ferns and bromeliads in montane forests in Bolivia (Kessler, in press).

To my knowledge, there are no studies quantifying the role of landslides in maintaining or enhancing biological diversity nor analyzing the occurrence of endemic plant species in particular successional habitats. Using a "space-for-time-substitution" (Picket 1989) I here compare the vegetation composition and richness of different successional forest stages in Carrasco National Park, Bolivia. The specific objectives of the present paper are to present a descriptive account of vegetation succession on natural landslides, emphasizing the role of bamboos and "viny" ferns, and, based on this successional scheme, to analyze quantitatively the effect of landslides on botanical diversity and endemism. For this purpose, endemism was measured as the number of squares occupied by each species in a 1° grid. With this approach, endemism is not determined by a rather arbitrary political or geographical cut-off value such as the 50,000 km^2 range size frequently used for birds (Terborgh & Winter 1983). Instead, every single species is given an endemism score, calculated as the inverse value of the number of degree squares occupied. A similar approach has been used by Fjeldså & Rahbek (1997) and Fjeldså et al. (1999) for Neotropical birds.

STUDY AREA

Carrasco National Park covers 6226 km^2 of the eastern Andean slope in the department of Cochabamba, Bolivia (Ergueta & Gómez 1997) (Fig. 1). Ranging from 300 m to 4500 m, it contains a complete set of elevational belts, many of which are in an almost pristine state, in particular those between 1000 m and 3000 m. The topography is extremely steep, with slope inclinations frequently ranging between 40° and 85° (Ibisch 1996). The geological substrate of the park consists mainly of sandstones, lutites and quartzitic rocks of the Devonian and Ordovician ages (Montes de Oca 1997, Ergueta & Gómez 1997).

The steep topography concentrates the convective precipitation in a narrow belt, making this one of the most humid regions in Bolivia. Ergueta & Gómez (1997) report a value of 4400 mm mean annual precipitation for the park, while Ibisch (1996) estimates a value of at least 3500 mm at 2200 m elevation in the valley of Sehuencas (Fig. 1). However, my own observations and those of my co-workers during nine weeks of fieldwork in both the dry (May to October) and the rainy (November to April) seasons suggest that slopes exposed to incoming clouds at mid-elevations (1000–3000 m) in the NW of the park receive considerably more precipitation than adjacent lowlands. Here, the climatic station at Villa Tunari (Fig. 1) reports an average of 5676 mm annual
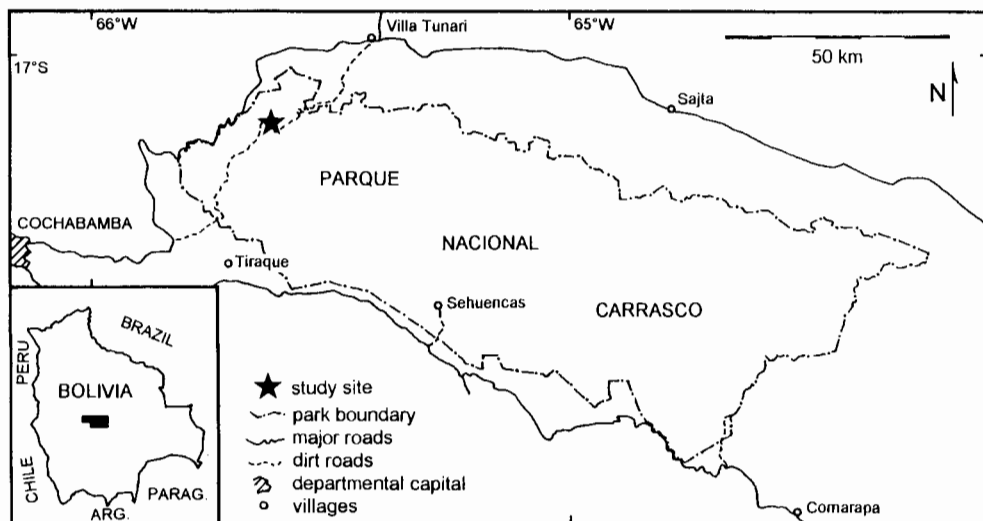
FIG. 1. Location of the study area in Carrasco National Park, dpto. Cochabamba, Bolivia.

precipitation (460 m elevation, 10 years data, Ibisch 1996). I would thus cautiously suggest that parts of the park may receive annual precipitations in excess of 8000 mm and that the lack of such high measurements is due to the absence of appropriately located climatic stations. Regardless of the exact absolute values for annual precipitation, there is no doubt that no month in the year receives less than 100 mm precipitation on average and that the climate can be considered perhumid (*sensu* Lauer *et al.* 1996).

METHODS

Field work was conducted from 23 June to 2 August 1996 along the old, now unused gravel road from Cochabamba city to Villa Tunari between 1900 m and 2800 m (17°07–09'S, 65°36–39'W), where steep slopes promote frequent landslides and where different successional stages were accessible. I established 38 non-permanent study plots of 400 m^2 each, mostly of square shape but occasionally in other shapes to minimize habitat heterogeneity. The elevational gradient of 900 m added considerable variability to the data which would ideally have been excluded from the sampling design. However, the extremely steep and inaccessible terrain restricted sampling to the proximity of the continuously ascending road (about 5% inclination on average) which made it impossible to access all successional

stages in a narrower elevational range. Access also limited the number of plots available in some successional stages. Despite these problems, there was no significant difference in the elevational distribution of the study plots in different successional stages (Fig. 2) (two-tailed least-squares ANOVA: $F_{5,32} = 0.463$,
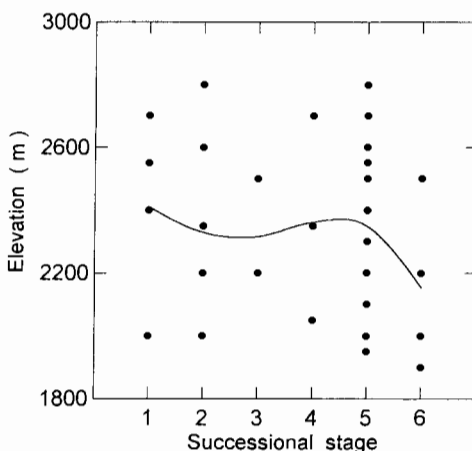

FIG. 2. Elevational distribution of the study plots by successional stages. The line fitted by distance-weighted least-squares smoothing closely corresponds to the mean elevational values of each successional stage.

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P = 0.801; pairwise two-tailed t-tests: P = 0.154 to P = 0.957).

The chronosequence of vegetation succession was established by visual comparison of landslides of differing age. Vegetation plots were assigned to one of the following successional stages on the basis of their vegetation structure: stage 1: only bryophytes and herbs present (N = 3 plots); stage 2: dominance of herbs, some shrubs present, but no trees (N = 6); stage 3: dominance of shrubs, small trees present (N = 3); stage 4: large pioneer trees (*Hedyosmum, Alnus*, tree ferns, etc.) present and dominant (N = 4); stage 5 (mature forest): full development of tall closed canopy, few bamboos or "viny" ferns (N = 18); stage 6 (senescenr forest): broken canopy, understory dominated by bamboos or "viny" ferns (N = 4).

For the descriptive account of the vegetarion structure of different successional stages, I estimated average height (to the closest 0.5 m below 3 m, to the closest 1 m at 3–10 m, to the closest 2 m above 10 m) and projected surface cover (to the closest 5% at < 30% cover, to the closest 10% at > 30% cover) of (1) terrestrial mosses and liverworts, (2) herbs, (3) shrubs (woody plants to 2 m tall), (4) understory trees (woody plants > 2 m tall, but not forming the canopy), (5) canopy trees, (6) bamboos, (7) ferns of the family Gleicheniaceae, and (8) ferns of the family Dennstaedtiaceae.

Due to the high species richness of the area and the difficulty of identification of many taxa, quantitative botanical sampling was restricted to three indicator groups: Bromeliaceae, Melastomataceae and Pteridophyta. These groups are physiognomically distinctive (making them easy to survey), have high species numbers (allowing for quantitative analyses), are comparatively easy to identify (by respective specialists, see acknowledgements), include terrestrial and epiphytic species, and are small (allowing for high species richness on fairly small plots). Presence/absence of all species was registered in each plot, treating terrestrial and epiphytic plants separately. (Ibisch 1996). All species encountered in the survey area (but not in every single plot) were collected and have been deposited at the Herbario Nacional de Bolivia (LPB, including all unicates), with the respective specialists, and at the Herbarium Göttingen (GOET).

For each successional stage I calculated three values: (1) *Species richness* was calculated as the mean number of species encountered per plot. (2) *Percentage of species not found in mature forest* was expressed as species recorded in a successional stage (except mature forest) that were not recorded in any mature forest plot as a percentage of the total species number in that successional stage. (3) The *endemism index E* was calculated for each plot as

$$E = (\sum_{i=1}^{n} a_i^{-1})\ n^{-1}.$$

where a is the range size of species i measured as the number of 1°-cells covered by the species' global range, and n is the number of species in the plot (cf. Williams & Humphries 1994). Distributions of all species of Bromeliaceae and Pteridopyhta encountered were compiled primarily from the following sources: Bromeliaceae: Dr. H. Luther pers. comm., Smith & Downs (1974–1979), Krömer *et al.* (in press); Pteridophytes: Dr. A.R. Smith pers. comm., Dr. R. Moran pers. comm., Dr. J.T. Mickel pers. comm., collections at The New York Botanical Garden (NY), the University Herbarium, Berkeley (UC), the Missouri Botanical Garden, St. Louis (MO) and the United States National Herbarium, Washington, D.C. (US), Tryon & Stolze (1989–1994), Davidse *et al.* (1995), Steyermark *et al.* (1995), and numerous generic treatments. Due to the large proportion of unidentified species, no such mapping was attempted for Melastomataceae. The resulting dot maps were interpolated on the basis of the species' ecological requirements and the distribution of main vegetation types (Hueck & Seibert 1981, Dinerstein *et al.* 1995) to obtain maps of the presumed natural ranges of the species. This mapping was conducted at a scale of 1° x 1°, the finest resolution at which such mapping can be conducted with reasonable confidence (Fjeldså & Rahbek 1997).

The above calculations were conducted independently for each indicator group and for terrestrial and epiphytic plants (individual species were included in both categories if growing epiphytically and on the ground). To correct for skewness, endemism values were subjected to logarithmic transformation. For stage 5, I also calculated the percentual change in species richness and endemism indices with elevation by linear curve fitting. Statistics were performed with SYSTAT 7.0 (SYSTAT 1997).

RESULTS

Successional dynamics and vegetation structure. Progressive landslide succession (stages 1-5) started with bryophytes, ferns (including numerous Lycopodiaceae, Gleicheniaceae, and *Elaphoglossum*), grasses (in

particular *Cortaderia*), Asteraceae and orchids (see also Ibisch 1996). More humid sites (either shaded south-exposed slopes or areas with seeping water) had dense mats of *Sphagnum* mosses and herbs. Dominant species in stages 2 and 3 included *Oyedaea boliviana* (Asteraceae), *Solanum* spp. (Solanaceae) and numerous Melastomataceae. Later, pioneer tree species, in particular *Hedyosmum racemosum* (Chloranthaceae), *Alsophila incana* (Cyatheaceae - on steep slopes), and *Alnus acuminata* (Betulaceae - on wet soils), formed 10 to 15 m tall secondary forests (Table 1). These were eventually invaded by the set of climax tree species to form mature forests (stage 5), including *Eugenia* spp., *Blepharocalyx salicifolius*, *Gomidesia barituensis* (all Myrtaceae), *Nectandra* cf. *laurel*, *N. obtusata*, *Ocotea* spp. (all Lauraceae), *Podocarpus rusbyi*, *P. oleifolius*, *P. glomeratus*, *Prumnopithys exigua* (all Podocarpaceae), numerous Araliacaea (*Schefflera*, *Oreopanax*, *Dendropanax*), the palm *Ceroxylon* sp., *Cedrela lilloi* (Meliaceae), *Clethra cuneata* (Clethraceae), *Crinodendron tucumanum* (Elaeocarpaceae), *Dicksonia sellowiana* (Dicksoniaceae), and *Weinmannia fagaroides* and *W. sorbifolia* (Cunoniaceae) (see also Ibisch 1996, Navarro 1997).

During early succession, bamboos occurred only along the edges of landslides and locally where debris piles with organic soil remained (Table 1). Throughout progressive succcession, bamboo vegetation cover

rarely exceeded 5%, reaching its highest average values of 4.9% in mature forest. Some fern species characteristically invaded open areas. These "viny" ferns included species of Gleicheniaceae (*Diplopterygium bancroftii* and several *Sticherus* species) and Dennstaedtiaceae (*Pteridium (aquilinum) arachnoideum*, *Histiopteris incisa* and particularly several species of *Hypolepis*). Some of these, especially taxa of Gleicheniaceae, reached high cover values during early and mid-succession, particularly in stages 2 and 3 (Table 1). In later stages of progressive succession their cover values decreased markedly. *Pteridium arachnoideum* was present in small numbers during early succession but was completely absent in well-developed forest, whereas other species of Dennstaedtiaceae occurred at low density in all successional stages.

In addition to the progressive succession described so far, there were also examples of regressive succession in the study area. At elevations between 1500 m and 3500 m, I observed patches of open forest with scattered large trees and a dense understory dominated by bamboo (mean cover 44.5%) and "viny" ferns, especially species of *Hypolepis* (mean cover 22.8%) (Table 1). These senescent forests superficially resembled anthropogenically disturbed or secondary vegetation after forest clearance (Figs. 3, 4). However, I believe that in the Carrasco region

TABLE 1. Height and cover of different life forms and selected plant groups in early successional (1), mid-successional (2: herb-dominated; 3: shrub-dominated), late successional (4), mature (5), and senescent (6) vegetation during natural landslide succession at 1900-2800 m in Carrasco National Park, Bolivia.

	1	2	3	4	5	6
Height (m)						
Bryophytes	0.04 ± 0.01	0.06 ± 0.03	0.05 ± 0.02	0.03 ± 0.02	0.05 ± 0.02	0.06 ± 0.02
Herbs	0.33 ± 0.03	0.62 ± 0.28	0.63 ± 0.26	0.65 ± 0.2	0.75 ± 0.25	0.54 ± 0.2
Shrubs	-	1.61 ± 0.41	1.5 ± 0.41	2.13 ± 0.68	2.08 ± 0.59	2.75 ± 0.75
Understory trees	-	-	-	5.75 ± 0.5	5.87 ± 0.73	4.67 ± 1.25
Canopy trees	-	-	4.33 ± 0.47	12.0 ± 3.5	13.56 ± 3.4	12.0 ± 2.5
Cover (%)						
Bryophytes	40.0 ± 10.0	87.5 ± 7.5	76.7 ± 18.4	32.0 ± 35.6	53.1 ± 22.0	20.0 ± 6.1
Herbs	30.0 ± 5.0	75.0 ± 14.1	83.3 ± 11.8	52.0 ± 16.0	57.8 ± 14.0	31.3 ± 13.5
Shrubs	-	15.0 ± 6.5	15.0 ± 4.1	42.0 ± 16.0	30.6 ± 17.3	70.0 ± 10.0
Understory trees	-	-	-	45.0 ± 23.0	39.3 ± 12.3	23.8 ± 10.1
Canopy trees	-	-	67.0 ± 2.4	65.0 ± 13.0	71.3 ± 19.0	57.5 ± 10.9
Bamboos	0	2.3 ± 2.0	0.1 ± 0.1	2.0 ± 1.4	4.9 ± 3.3	44.5 ± 11.4
Gleicheniaceae	0.5 ± 0.5	6.2 ± 5.8	12.3 ± 7.9	1.2 ± 1.8	0.5 ± 0.7	4.3 ± 3.5
Dennstaedtiaceae	0.5 ± 0.5	3.2 ± 2.8	2.5 ± 1.8	1.4 ± 1.9	2.0 ± 1.5	22.8 ± 10.5
N =	3	6	3	4	18	4

FIG. 3. Perhumid montane forest at about 2900 to 3300 m in Carrasco National Park, showing recent (Lr - not studied) and partially overgrown landslides (Lo - stages 1-3), mature forest (M - stage 5), and senescent forest (stage 6) with abundant bamboo (Sb) and ferns (Sf).

these forests were formed by natural processes because they frequently occurred in irregularly formed and spaced patches, and often on very steep inaccessible slopes, in a region with no signs of current or past human settlements (Fig. 3). Their shape thus differed from the usual rectangular forms of man-made clearings observed elsewhere in the Bolivian Andes. Also, there were always large trees scattered irregularly throughout the bamboo or fern patches, often in fairly high densities. Elsewhere, I have not observed left-over trees (except an occasional palm) in man-made clearings in montane forests.

I suggest that these senescent forests are formed when one or a few trees collapse in an area of mature forest. Bamboos and "viny" ferns, which occur as subordinate components of the mature forests, quickly invade the light gap, forming such a dense vegetation layer that the regeneration of woody plants, especially trees, is inhibited. As more and more canopy trees die, larger areas become dominated by the viny species.

Species richness and endemism. In total, 22 species of bromeliads, 51 of Melastomataceae and 189 of Pteridophyta were recorded in the 38 vegetation plots. Of these, 18 bromeliads and 103 ferns were growing epiphytically, whereas 11 bromeliads and 142 ferns were growing terrestrially. Seven bromeliads (32% of total species number) and 56 ferns (30%) were found both as epiphytes and as terrestrial species. All Melastomataceae were terrestrial.

With the exception of endemism among epiphytic ferns and terrestrial bromeliads, all study groups showed changes in species richness and endemism with increasing elevation from 1900 m to 2800 m by −25% to +350% (Table 2). This variability added considerable variance to the values of richness and endemism in the different successional stages, but since the stages were distributed roughly equally across elevation (Fig. 2) these changes cannot account for differences detected among successional stages. It may, however, be no coincidence that differences in endemism were significant for epiphytic

FIG. 4. Senescent perhumid montane forest at 1950 m in Carrasco National Park with scattered epiphyte-laden canopy trees and a dense understory dominated by *Hypolepis nigrescens* and *H. parallelogramma* (Dennstaedtiaceae).

TABLE 2. Probability levels (P) of differences in species richness and endemism indices between all successional stages (two-tailed least-squares ANOVA) and percentage change in richness and endemism with increasing elevation from 1900 m to 2800 m in successional stage 5.

	P	elevational change (%)
Species richness		
epiphytic Pteridophyta	< 0.001	− 27
terrestrial Pteridophyta	0.188	− 27
epiphytic Bromeliaceae	< 0.001	− 54
terrestrial Bromeliaceae	< 0.001	+ 350
Melastomataceae	0.007	− 38
Endemism index		
epiphytic Pteridophyta	0.005	± 0
terrestrial Pteridophyta	0.186	− 25
epiphytic Bromeliaceae	0.126	− 18
terrestrial Bromeliaceae	0.002	± 0

ferns and terrestrial bromeliads (which showed no elevational effect), but not for terrestrial ferns and epiphytic bromeliads (which showed a clear elevational effect). Small sample size precluded conducting a similar analysis for the other successional stages or using multivariate statistics for all stages across elevation.

Epiphytic pteridophytes, terrestrial, and epiphytic bromeliads, and Melastomataceae all showed a significant increase in species richness from successional stage 1 to stages 3 to 5 (Table 2, Fig. 5). Terrestrial pteridophytes had maximum richness in stage 3, but this was not significantly different from other stages. All groups showed a decline in species richness from stage 5 to stage 6 which was almost statistically significant in Melastomataceae (two-tailed t-test, $P = 0.07$) but not significant in all other groups (two-tailed t-tests, $P = 0.13$ to $P = 0.63$).

Early successional stages were composed mainly of species not found in mature forest (Fig. 6). In stage 1, this group included 81.3% of the terrestrial ferns
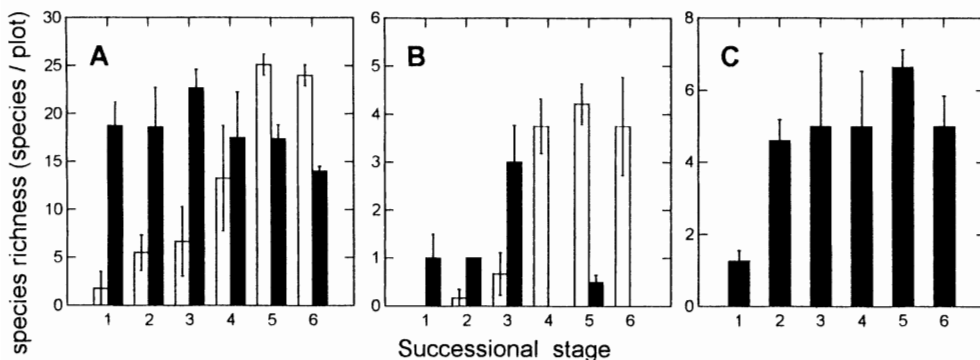
FIG. 5. Species richness of epipyhtic (white bars) and terrestrial (black bars) species of Pteridophyta (A), Bromeliaceae (B), and Melastomataceae (C) in six different successional vegetation stages at 1900 to 2800 m in a perhumid montane forest in Carrasco National Park, Bolivia, in vegetation plots of 20 x 20 m.

and 100% of both Melastomataceae and terrestrial bromeliads. Lower, but still important, values were also found for terrestrial species in stages 2 and 3. Stages 4 and 6 contained only a few species not recorded in mature forest. Even these few species were probably missed in mature forest as a result of sampling stochasticity. When grouped by life form, 58.5% of all terrestrial herbs (averaging bromeliads and ferns), 10% of the woody plants (Melastomataceae) and 1.3% of all epiphytic species (averaging bromeliads and ferns) were recorded only in stages 1 to 3 (Table 3). The values for terrestrial herbs and woody plants differed significantly from expected values if species were randomly distributed across the succes-

TABLE 3. Percentage of all vascular plant species representing respective plant life forms (A) (after Ibisch 1996), percentage of species registered only in successional stages 1–3 (B) (this study), and percentage of all vascular plants restricted to stages 1–3 (C = A x B / 100) for three groups of plant life forms during landslide succession in a humid montane forest at 1900–2800 m in Carrasco National Park, Bolivia.

	A	B	C
Terrestrial herbs	30	58.5	17.5
Woody plants	35	10	3.5
Epiphytes	35	0[a]	0
Sum	100	–	21.0

[a] Observed value of 1.3% was not significantly different from random value.

sional stages (two-tailed χ^2-tests, $P < 0.01$, $P < 0.05$ respectively). The value for epipyhtic species was not significant (two-tailed χ^2-test, $P = 0.87$), suggesting that epipyhtic species not encountered in stage 5 were simply missed as a sampling artifact, i.e., they occurred in mature forest but were not included in the study plots.

All study groups showed a similar pattern of endemism: high values in stages 1 and 2, lower values in stage 3, a noticeable increase in stages 4 and 5, and a decrease in stage 6 (Fig. 7). These differences were significant for epiphytic ferns and terrestrial bromeliads (Table 2). Stage 3 had significantly lower values of endemism (at a significance level of $P \leq 0.025$ due to Bonferroni correction) than stage 5 for epiphytic ferns (two-tailed t-test, $P = 0.004$) and terrestrial ferns (two-tailed t-test, $P = 0.02$), and almost so for terrestrial Bromeliaceae (two-tailed t-test, $P = 0.03$) and epiphytic Bromeliaceae (two-tailed t-test, $P = 0.06$), whereas the decline in endemism from stage 5 to stage 6 was in no case statistically significant (two tailed t-tests: $P = 0.12$ to $P = 0.97$).

DISCUSSION

Successional dynamics and vegetation structure. Generally speaking, progressive landslide succession followed the pattern described by Garwood (1985) in Panama and by Stern (1995) in Ecuador. The most important differences were detected in the role of bamboos and "viny" ferns during succession. In the Carrasco region, "viny" fern species of the family Gleicheniaceae, and to a lesser degree bamboos and

Dennstaedtiaceae, occurred during progressive succession but did not suppress woody plant regeneration at this stage. During regressive succession, however, they formed dense thickets which inhibited the growth of other woody species. This suggests that in the study area these species need a combination of well-developed organic soils and good light conditions to be able to dominate a plant community.

Apparently, the ability of bamboos to colonize raw soils, to invade gaps and to prevent tree regeneration varies regionally and between bamboo species. Whereas in the Chilean Andes Veblen & Ashton (1978) found that *Chusquea* bamboo requires organic soil, Stern (1995) observed that bamboo invades fresh landslides in the Ecuadorian Andes, thus limiting the growth of other plants. Also, while the inhibition of tree regeneration by bamboos has been reported from mature forests in southern Chile (Veblen 1989), Ecuador (Stern 1995), Venezuela

(Meier 1998), and Costa Rica (Widmer 1998), in the Peruvian Andes, Young (1991) found no effect on tree community composition by a *Chusquea* species. The limited number of studies available are insufficient for making generalizations about the conditions favoring the different ecological responses of bamboos.

Ferns have so far received much less attention than bamboos as aggressive invasive species in natural forest communities. Bracken ferns (*Pteridium* spp.) are well-known invasive species in anthropogenically disturbed habitats (Cartledge & Carnahan 1971). In the Carrasco area, *Pteridium arachnoideum* was present, but did not reach the local dominance observed in man-made clearings elsewhere in the Bolivian Andes (pers. obs.). *Pteridium* is probably favored in the Andes by burning (B. León, pers. comm., pers. obs.). Under natural conditions with few or no fires, the ecological niche of *Pteridium* as
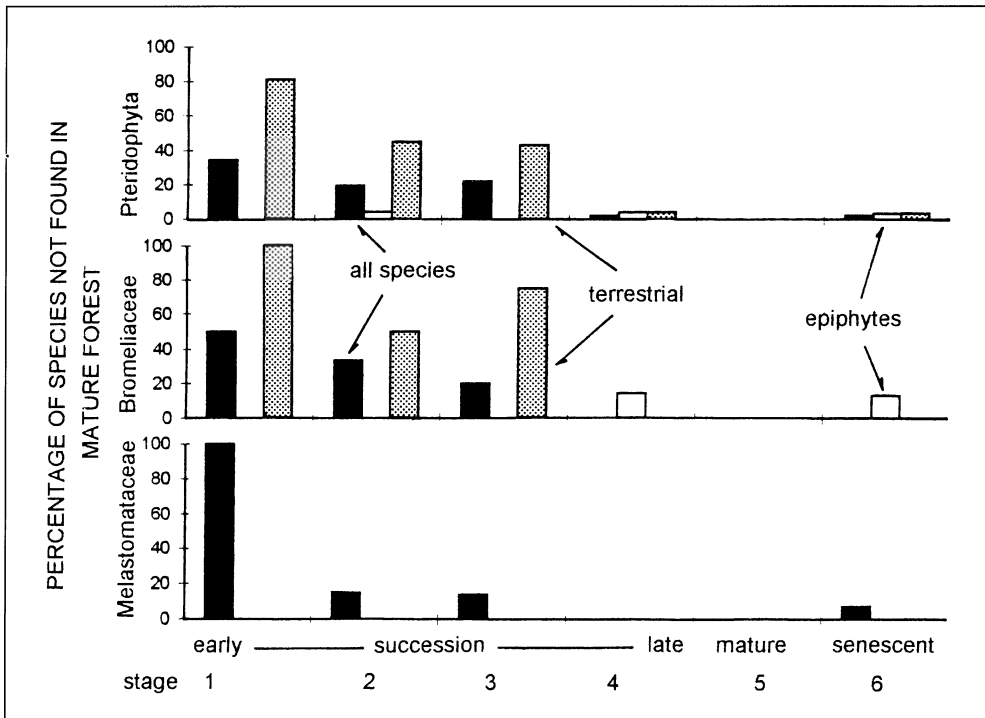

FIG. 6. Percentage of pteridophyte, bromeliad and Melastomataceae species not recorded in mature forest of the total number of species recorded in different stages of vegetation succession on natural landslides. For pteridophytes and bromeliads black bars correspond to all species, white bars to epiphytic species, and gray bars to terrestrial species.
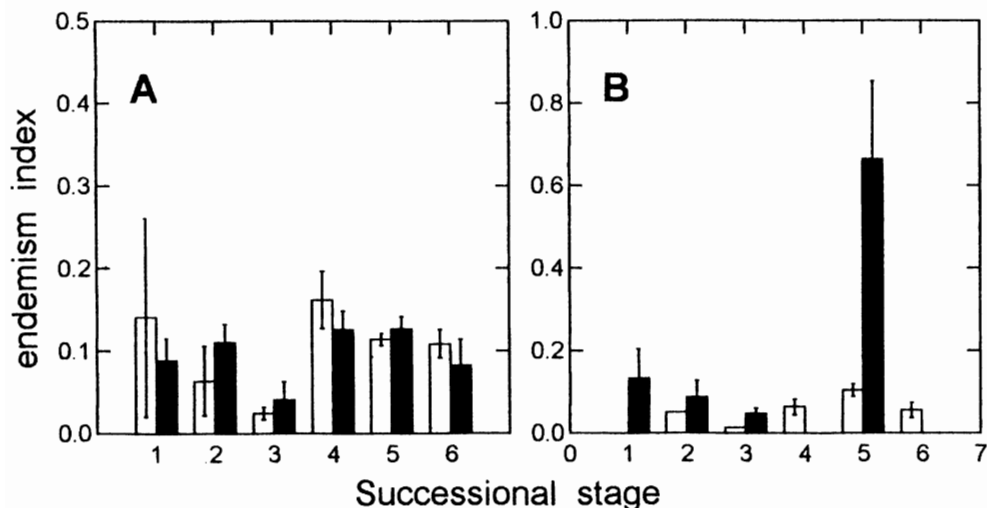
FIG. 7. Endemism index of epiphytic (white bars) and terrestrial (black bars) species of Pteridophyta (A) and Bromeliaceae (B) in six different stages of vegetation succession on natural landslides. Higher values of endemism index indicate a stronger representation of narrowly distributed species.

an aggressive invasive species is filled by the genus *Hypolepis*.

I have not observed similar senescent forests elsewhere in the Bolivian Andes, suggesting that some special condition of the Carrasco region, most probably the high rainfall, causes this phenomenon. On the other hand, bamboo- and liana-dominated lowland forests are known from Amazonia (Prance 1987, Foster *et al.* 1994), where landslides are absent. These forests currently seem to be slowly expanding their range at the expense of more diverse mixed forests, the occurrence of which might depend on medium- or long-term disturbances. Similar patterns have been observed for tropical lowland forests dominated by single tree species (Hart *et al.* 1989). Thus, it seems plausible that the senescent forests of the Carrasco region are dominated by superior competitors which, in the absence of any further disturbance, would eventually cover large areas. The dominance of bamboos and ferns in senescent forests may be broken by three factors: (a) depletion of soil nutrients and subsequent population collapse, (b) in the case of bamboos, slow regeneration after mass monocarpic flowering events (Janzen 1976, Clark 1989, Clark *et al.* 1989), and (c) destruction of senescent forests by landslides, which seems likely given the massive accumulated organic soil layers which frequently become saturated with water (Whitmore 1975).

I here present the hypothesis that bamboo- and fern-dominated forests in the Carrasco region represent senescent forests in order to stimulate future research on tropical montane forest dynamics and as a conceptual frame for the analysis of diversity and endemism patterns found in the present study. Long-term observations or the analysis of aerial image time-series will be necessary to test this hypothesis.

Species richness and endemism in different successional stages. Overall, levels of species richness and endemism showed high standard deviation values (25–105% of the mean). This variance was certainly a result of the elevational range covered by the study and of site-specific differences between the plots such as slope inclination and aspect. In combination with low sample size, this variance made statistical analysis difficult. For this reason, convergent trends among different study groups, e.g., the decline in species richness from stage 5 to stage 6 observed in all study groups, will be discussed as "real" patterns, even if the difference in every single case was not statistically significant at $P \leq 0.05$ (see, e.g., Scheiner (1993) for the rationale that the significance level of $P \leq 0.05$ should not be treated as a fixed limit).

The increase in species richness through progressive succession is not surprising, and corresponds to primary successional dynamics observed elsewhere

on raw soils (Crocker & Major 1955, Walker *et al.* 1981). The rarity of epiphytic ferns and bromeliads during early succession certainly reflects the lack of suitable growth sites. The relatively higher species richness of epiphytic ferns compared with epiphytic bromeliads during mid-succession may be due to their smaller size (e.g., species of Grammitidaceae, *Hymenophyllum* or *Polypodium*) which enables them to colonize smaller plants (Ibisch 1996).

The decline in species number in senescent forests is in accordance with theories of successional dynamics in which superior competitors displace species with lower competitive ability in the absense of further disturbance (Huston & Smith 1987). Not unexpectedly, this decline was more pronounced among terrestrial species (which were directly affected by the competion from aggressive bamboos and ferns) than among epiphytic species (whose decline in species number was mostly a result of a lower availability of growth sites). This study therefore provides an example where species richness is highest during mid-stages of succession, being lowest at both ends of the development. Similar patterns have been described for intermediate levels of disturbance (Connell 1978, Huston 1979), biomass (Bond 1983) and soil fertility (Walker *et al.* 1981). These patterns are highly scale dependent (Cooper 1913, Huston 1994). If, for example, only a particular spot in Carrasco National Park were observed over time, then a pattern of highest diversity in mature forest would emerge, as illustrated in figure 5. This would be an example of highest diversity at *intermediate age*. If a larger area of some hectares or a few square kilometers is considered, then total species richness in this area would be highest at some level of *intermediate disturbance*. Areas with no landslides at all would be dominated by mature or even senescent forests and would lack colonizing species. On the other hand, excessive landslides would reduce or eliminate mature forest, greatly reducing overall species numbers. In even larger areas (tens to thousands of square kilometers), such extreme situations (total lack or absolute dominance of landslides) do not occur. At this spatial level, the number of species is unlikely to be affected by the frequency of landslides. These spatial effects need to be borne in mind when considering the effect of landslides on local or regional plant species richness.

I estimate that about one fifth (21.0%) of all vascular plant species occurred only in successional stage 1 to 3, almost exclusively among terrestrial taxa

(Table 3). This number is only a rough figure, however, since it is not known how representative the study groups are of the overall flora. In humid montane forests in Ecuador and Peru, these groups comprise about 20–23% of all vascular plant species (Young & León 1990, León *et al.* 1992, Jørgensen & Ulloa Ulloa 1994). A further complication is posed by the possibility that species which were recorded in early successional stages and in mature forest are not capable of maintaining viable populations in one of these habitats and depend on continuous dispersal from their core habitats (mass effect *sensu* Shmida & Whittaker 1981, sink effect *sensu* Shmida & Ellner 1984). In this case, the proportion of species restricted to early successional habitats may be even larger than estimated here. In addition to ferns and bromeliads, this group of landslide-dependent taxa may include species of Asteraceae, Ericaceae, Poaceae, Polygonaceae, and Scrophulariaceae, among others.

There were almost no epiphytic species restricted to early successional stages. This is not surprising, considering the paucity of suitable habitats and bearing in mind that among epiphytes niche selection takes place mostly within the structural habitats provided by the trees and forests themselves (Johansson 1974, Ibisch 1996) rather than between forest types of different age. Colonization and succession in epiphyte communities takes place continuously on newly developing branches of every single tree. Overall, epiphyte diversity appeared to be rather independent of landslide dynamics.

The high levels of endemism in early successional stages (1 and 2) and in mature forest (stage 5) compared to mid-succession (stage 3) and senescent forests (stage 6) are intriguing. Apparently, early natural succession is not directly comparable to early succession in human-disturbed habitats, where endemism among birds (Stotz *et al.* 1996, Laurance & Bierregaard 1997) and plants (Kessler, in press) is lower than in adjacent mature forest. This difference may correspond to the distinction between primary succession on raw soils (e.g., on landslides) and secondary succession on developed soils (e.g., on man-made clearings).

High levels of endemism may be favored by the comparatively high stability of open habitats and mature forests. While early landslide vegetation is clearly not a stable habitat in itself, it shares a number of species with open habitats on steep rock faces which are found scatterd throughout the area (unpubl. data) and which probably represent stable habitats where

endemic species can maintain viable populations. Saxicolous species are well known for their tendency towards localized distributions and high endemism (Ibisch 1996). Opposed to this, mid-successional habitats are inherently unstable environments, representing a transitition stage during succession and lacking a stable ecological counterpart. Such unpredictable environmental conditions should favor species with high dispersal abilities which would therefore tend to be widespread. Such species would also be likely candidates to form secondary vegetation during man-induced succession. These hypotheses should be tested in areas where natural landslide succession and anthropogenic succession can be studied in close proximity.

The decrease in endemism in senescent forests compared with mature forests may be a result of competitive exclusion of endemic species by widespread taxa. This assumption is supported by the observation that in a humid montane forest area about 130 km west of the present study site, endemism of fern and bromeliad communities increased in forests with slight human disturbance compared with natural forests (Kessler, in press). This suggests that plant species with restricted ranges tend to be competitively inferior to widespread species, thus being unable to expand their natural ranges and being favored by a certain level of disturbance which disrupts competitive interactions. In this case, natural landslides might represent an important factor in maintaining non-equilibrium conditions.

The apparent contradiction between the importance of stability against disturbance in maintaining high levels of endemism must be considered in the light of varying spatial and temporal scales (Huston 1979, 1994). Endemic species appear to require long-term *predictable*, i.e., stable conditions (cf. Fjeldså *et al.* 1999) which may include short-term *dynamic*, i.e., unstable processes such as landslides.

Summarizing, landslides in the study area affect plant diversity in various ways at different levels of diversity: At the level of beta-diversity (between-habitat diversity *sensu* Cody 1986) they provide habitat for about 20% of the vascular plant flora. At the level of alpha-diversity (within-habitat diversity) they may play a role in the destruction of senescent forests and may thus support the maintenance of species-rich mature forests. Finally, if the patterns of endemism found in the study area hold true over larger geographical regions, then the maintenance of early successional vegetation and of mature forests,

both of which have high endemism, would imply a strong geographical turnover of species composition over larger areas, corresponding to high gamma-diversity (*sensu* Cody 1986).

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